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Cryptic Species in the Fern *Ceratopteris thalictroides* (L.) Brongn. (Parkeriaceae). IV. Taxonomic Revision

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Herbarium specimens referable to *Ceratopteris thalictroides* in the sense of Lloyd were examined and the following cryptic taxa were recognized; *C. thalictroides*, *C. gaudichaudii* var. *gaudichaudii*, *C. gaudichaudii* var. *vulgaris* (var. nov.), *C. oblongiloba* (sp. nov.), and *C. froesii*. Compared with *C. thalictroides* s.str., *C. gaudichaudii* var. *vulgaris* is basically characterized by short stipes and dense pinnae, while *C. oblongiloba* is characterized by dense pinnules and narrowly oblong terminal lobes. A key to distinguish them and descriptions of the taxa are presented.

Key words: *Ceratopteris froesii*, *Ceratopteris gaudichaudii*, *Ceratopteris gaudichaudii* var. *vulgaris*, *Ceratopteris oblongiloba*, *Ceratopteris thalictroides*, cryptic species, Parkeriaceae, referential diagnostic character

The genus *Ceratopteris* (Parkeriaceae) is a group of semi-aquatic or aquatic annual ferns distributed in the tropics, subtropics and warm-temperate regions. The genus was described by Brongniart in 1821, based on *Acrostichum siliquosum* L. and *A. thalictroides* L. Eleven species have been described so far. Species recognition, however, has been confused due to their high polymorphism. In the extreme, all have been regarded as a single species, *Ceratopteris thalictroides* (*e.g.*, Christensen 1906).

The most comprehensive monograph of *Ceratopteris* was published by Lloyd (1974). He combined the eleven species into four: 1) *Ceratopteris cornuta* (Pal. Beauv.) Le Prieur, 2) *C. pteridoides* (Hook.) Hieron. including *C. lockhartii* (Hook. & Grev.) Kunze and *C. parkeri* J. Smith, 3) *C. richardii* Brongn. including *C. deltoidea* Benedict, and 4) *C. thalictroides* (L.) Brongn. including *C. froesii* Brade, *C. gaudichaudii* Brongn., *C. siliquosa* (L.) Copel. and *Ellobocarpus oleraceus* Kaulf.

Of the above four species, *Ceratopteris thalictroides* is particularly polymorphic and includes many forms that should be described taxonomically. In this, Lloyd (1974) noted that *C. thalictroides* s.lat. includes several forms which may deserve formal taxonomic recognition at the infraspecific level. The forms cited are as follows: Japanese plants that are extremely small, Japanese plants that are far larger, Guam plants named *C. gaudichaudii*, which are floating and have attenuated segments of leaves, Brazilian plants named *C. froesii*, which are very small and have simple to trilobed leaves, and Surinam plants that have long stipes and slightly dissected, round to ovate pinnae. Whether at the specific or infraspecific level, taxonomic description should be given to these forms.

In our first paper on cryptic species in *Ceratopteris thalictroides* (Masuyama *et al.* 2002), we pointed out that *C. thalictroides* in the sense of Lloyd contains at least three entities that should be regarded as species because of differences in nucleotide sequence of chloroplast DNA and in allozyme composition coupled with cross-sterility. We referred to them as the south type, the north type, and the third type.

In the second paper (Masuyama & Watano 2005), we showed that the north type and the third type are tetraploid with $2n = 156$ chromosomes while the south type is hypotetraploid with $2n = 154$, and suggested that *C. thalictroides* in the sense of Lloyd might be tetraploid, whereas the other three species might be diploid.

The third paper (Masuyama 2008) reported that the three types showed continuous variation in morphology and had no fine diagnostic character, but some characters exhibited ranges of variation that were statistically different among the types, when they were cultivated under common conditions favorable for growth. Those characters were called referential diagnostic characters. The paper suggested that, although the ranges of variation of those characters partially overlap among the three types, it is possible to classify specimens into the three types by applying those characters collectively. In particular, the following five characters are visually distinct: 1) the relative length of stipe to blade, 2) the degree of dissection, 3) the segment density on rachis and pinna-rachis (the ratio of the mean distance among pinnae to the blade length and the ratio of the number of segments to the length of the basal pinna, respectively, in the statistical treatment), 4) the elongation degree of terminal lobes (the ratio of length to width of oblong terminal lobes), and 5) the number of annulus cells. Although these characters are useful for identifying average individuals, they are not always effective for identifying well- or poorly-grown individuals or those with special ecologically influenced habits, such as floating forms. For those individuals, only presumptive identification may be possible even if these characters are applied collectively.

In the present study, we examined specimens referable to *Ceratopteris thalictroides* in the sense of Lloyd in BM, BO, GUAM, KYO, LINN, NY, P, PNH, TI, TNS, UC and US, and tried to classify them into the three types by using the referential diagnostic characters. As a result, we recognized the following five taxa in *C. thalictroides* in the sense of Lloyd.

1) *Ceratopteris thalictroides* (L.) Brongn. corresponding to the south type of Masuyama *et al.* (2002);

2) *C. gaudichaudii* var. *vulgaris* (var. nov.) corresponding to the north type of Masuyama *et al.* (2002), which is represented by small Japanese plants noted by Lloyd (1974);

3) *C. gaudichaudii* Brongn. var. *gaudichaudii*, which has the same *rbcL* gene sequence and chromosome number as var. *vulgare* but differs in morphology;

4) *C. oblongiloba* (sp. nov.) corresponding to the third type of Masuyama *et al.* (2002), to which Lloyd (1974) did not refer;

5) *C. froesii* Brade, which differs in morphology from the above four taxa.

Key to species of *Ceratopteris thalictroides* sensu Lloyd

Since characters cited below are not rigid but referential diagnostic ones, it is necessary to check as many characters as possible and to base determinations on multiple criteria.

1. Sterile leaves to 3 cm long, simple to trilobed, lobe-apex obtuse to rounded .... 5. *C. froesii*
1. Sterile leaves mostly more than 3 cm long, bipinnatifid or more compound, lobe-apex not rounded
  2. Sterile leaves oblique or upright, herbaceous, stipes sometimes longer than blades, pinnae rather sparse on rachis, pinnules not dense on pinna-rachis, lobes entire, lobe-apex mostly obtuse, terminal lobes ovate to oblong; fertile leaves dissected to 5 times; annulus cells 25–40; chromosomes $n = 77$, $2n = 154$ .... 1. *C. thalictroides*
  2. Sterile leaves oblique or patent, softly herbaceous, stipes shorter than blades, pinnae rather dense on rachis, pinnules dense or not on pinna-rachis, lobes entire or dentate, lobe-apex acute or obtuse, terminal lobes ovate to narrowly oblong; fertile leaves dissected to 4 times; annulus cells 35–60; chromosomes $n = 78$, $2n = 156$

3. Sterile leaves highly gemmiferous, pinnules not dense, lobes often dentate, lobe-apex acute, terminal lobes narrowly deltoid to narrowly oblong .... 2. *C. gaudichaudii* var. *gaudichaudii*
3. Sterile leaves slightly gemmiferous, pinnules dense or not, lobes entire, lobe-apex acute or obtuse
   4. Pinnules not dense, terminal lobes ovate to oblong .... 3. **C. gaudichaudii** var. **vulgaris**
   4. Pinnules dense, terminal lobes small, narrowly deltoid to narrowly oblong ...... 4. **C. oblongiloba**

1. **Ceratopteris thalictroides** (L.) Brongn.

C. thalictroides (L.) Brongn., Bull. Sci. Soc. Philom. Paris, sér. 3, 8: 186 (1821); Christensen, Ind. Filicum: 169 (1906), p.p.; Benedict, Bull. Torrey Bot. Club 36: 467 (1909); Fosberg, Amer. Fern J. 48: 35 (1958); De Vol, Taiwania 13: 2 (1967), p.p.; Lloyd, Brittonia 26: 148 (1974), p.p. –*Acrostichum thalictroides* L., Sp. Pl.: 1070 (1753). –*Pteris thalictroides* (L.) Swartz, J. Bot. (Schrader) 4: 651 (1801). –*Teleozoma thalictroides* (L.) R. Br., Franklin's Narrative of Journey: 767 (1823). –*Furcaria thalictroides* (L.) Desv., Prod. Fam. Foug. 6: 292 (1827). —*Lectotype.* Ceylon, *Hermann Herb. 3: 42, specimen 377* (BM [photo!]).

Acrostichum siliquosum L., Sp. Pl.: 1070 (1753). –*Pteris siliquosa* (L.) P. Beauv., Fl. Oware 1: 63 (1804). –*Ceratopteris siliquosa* (L.) Copel., Gen. Fil.: 83 (1947). —*Lectotype.* Ceylon, *Hermann Herb. 2: 59, specimen 376* (BM [photo!]).

Ellobocarpus oleraceus Kaulf., Enum. Fil. 148 (1824), nom. superfl.

Pteris succulenta Roxb. ex Griff., Cal. J. Nat. Hist. 4: 508 (1844). –*Ceratopteris succulenta* (Roxb.) Fraser-Jenk., Tax. Rev. Three Hundred Ind. Subcont. Pterid. Rev. C. List: 415 (2008). —*Lectotype.* India, *Smith Herbarium 1622-39* (LINN [photo!])

Plants annual, semi-aquatic, rooting. *Rhizomes* reduced. *Roots* at stipe base. *Scales* sparse on stipe, brownish-hyaline, sessile, broadly ovate to peltate with gently curved margins, lamina thin, composed of sinuous cells. *Leaves* dimorphic. *Sterile leaves* 10–50 cm long, held obliquely to upright, green, herbaceous, gemmiferous at sinuses of segments; stipes 2/3–1 2/3 length of blade, semicircular to trapezoid in cross section; blades 5–20 cm long, 4–10 cm wide at base, narrowly triangular, 2–4-dissected, 1-pinnate; pinnae 3–9 pairs, alternate, basal pinnae 2–7 cm long, 1.5–5 cm wide at base, triangular to narrowly triangular, with short stalk; pinnules 0–4 pairs, alternate, base broadly decurrent; terminal lobes entire, ovate to deltoid to oblong, apex mostly obtuse; oblong terminal lobes to 2 cm long, 0.5 cm wide; veins anastomosing, without veinlet in areole. *Fertile leaves* 15–80 cm long, mostly upright, brownish at maturity; stipes 1/2–1 1/2 length of blade; blades 6–40 cm long, 4–20 cm wide at base, narrowly triangular, 3–5-dissected, 2–4-pinnate; pinna 5–12 pairs, with short stalk, alternate, basal pinnae 3–16 cm long, 3–14 cm wide, triangular to narrowly triangular; terminal lobes to 7 cm long, 0.2 cm wide, linear, margin thin, reflexed toward costa enclosing sori. *Sporangia* subsessile; annulus vertical, with 25–40 broad incrassate cells and 8–10 broad lip cells. *Spores* 32 per sporangium, tetrahedral, 90–140 μm in distal diam., with thick parallel-muri on surface. *Chromosomes* $n = 77$, $2n = 154$; tetraploid. *Nucleotide sequence of rbcL gene* AB059574 registered in INSD (International Nucleotide Sequence Databases).

Japanese name. Mizuwarabi (Matsumura, 1904).

Distribution. **Asia**: Brunei, China (S.), India, Indonesia (Java, Kalimantan, Sulawesi, Sumatra), Japan (S.), Malaysia (Malay P., Sabah), Philippines (Luzon, Mindanao), Sri Lanka, Taiwan, Thailand (S., Malay P.). **Central America**: Costa Rica, Panama. **Oceania**: Australia (N.), Guam, Hawaii, Palau, Papua New Guinea, Truck Isl., Yap Isl.

Habitat. Swamps, small streams, irrigation ponds, irrigation ditches, taro patches, rice paddies.

Representative specimens examined. AUSTRALIA: W. Australia, Wyndham Bay, *Britton s.n.* (NY).

BRUNEI: Kuala Belait, *Van Niel 3519* (KYO).

CHINA: Hong Kong, Un-Loon, *Taam 1580* (UC, US).

COSTA RICA: Cartago, *Beitel 77156* (NY).

INDIA: Bengal?, *Roxburgh, Smith Herb. 1622-38 & 39* (LINN); Central Prov., Raipur, *Marten s.n.* (KYO); Courtallum, *Le Loy 36* (NY); Mysore, Hassan, *Saldanha & Ramamoorthy 1216* (US).

INDONESIA: Celebes, Tataaran, *Alston 16337* (BO);

Java, Bonderrso, *Backer s.n.* (BO); Kalimantan, Banjelmasin, *Murata & al. B-4526* (KYO); Sumatra, Tandjungpura, *Iwatsuki & al. 415* (BO).

JAPAN: Okinawa, Iriomote Isl., Komi, *Masuyama 1781* (TNS); Okinawa, Iriomote Isl., Ootomi, *Masuyama 1192* (TNS); Okinawa, Iriomote Isl., Sonai, *Masuyama 1140* (TNS); Okinawa, Iriomote Isl., Urauchi, *Masuyama 814* (TNS); Okinawa, Ishigaki Isl., Motonagura, *Masuyama 1228* (TNS); Okinawa, Miyako Isl., Shimajiri, *Shimabuku 3877* (KYO); Okinawa, Okinawa Isl., Kunigami, *Sakaguchi s.n.* (KYO); Okinawa, Okinawa Isl., Onnason, *Masuyama 791* (TNS).

MALAYSIA: Mata Isl., Timbun, *Agama 7652* (PNH); Penang, *Melesworth-Allen 2764* (US).

PALAU: Babeldaob Isl., Ngatpang, *Bouden-Kerby & Raulerson LR5728* (GUAM); Palau Isl., *Koizumi s.n.* (TI).

PANAMA: Penonome, *Williams 469* (NY, US).

PAPUA NEW GUINEA: Central Dist., Kairuku, *Darbyshire 818* (UC, US).

PHILIPPINES: Luzon, Zambales, *Fox s.n.* (PNH); Mindanao, Davao, *Copeland 425* (US); Mindanao, San Ramon, *Copeland 1460* (NY, TI); Samar Isl., Guian, *Wagner 3587* (UC, US).

SRI LANKA: Western, Southern Prov., *Hope s.n.* (NY).

TAIWAN: Hokuto, *Faurie 236* (KYO); Taipei, *Sasaki s.n.* (TI).

THAILAND: Ayuthia, Pathum Thani, *Tagawa & Iwatsuki T286* (KYO); Haadya, *Melesworth-Allen 994* (US); Kanchanaburi, Thong Pha Phum, *Shimizu & al. T-21907* (KYO); Phattalung, Nakawn Sritamarat, *Tagawa & Yamada T224* (TI).

TRUK: Truk Isl., Puluwat, *Manner & Mallon HM118* (GUAM).

YAP: Central Yap, Mabu, *Cushing 565* (GUAM, NY).

Notes. Ceratopteris thalictroides corresponds to the south type reported by Masuyama *et al.* (2002). The type specimen of *Acrostichum siliquosum* is merely a part of a fertile leaf, but, as Benedict (1909) regarded, it is judged to be *C. thalictroides* because of the long stipe. The lectotype of *Pteris succulenta* designated by Morton (1974) (*Smith Herb. 1622-39* [LINN]) is judged to be *C. thalictroides*, though the Roxburgh's drawing of *P. succulenta* (Roxburgh t108; see Fraser-Jenkins, 2008) is similar to the north type of Masuyama *et al.* (2002), another species described below. Although Lloyd (1974) listed *Najas obvoluta* as a synonym of *C. thalictroides*, it is a member of the angiosperm family Hydrocharitaceae.

Plants of Guyana have the same chloroplast DNA sequence and chromosome number ($2n = 154$) as the south type (Masuyama *et al.* 2002, Masuyama & Watano 2005). However, they differ in the allelic composition of nuclear DNA (Adjie *et al.* 2007) and sterile-leaf morphology; the stipes of Guyana plants are remarkably long, the blades, except for the basal pinnae, are dissected only one or two times, and the lobes are round to ovate (*Persand 188* [NY]). *Maquire & Stahel 22719* (NY) from Surinam cited by Lloyd (1974) shows the same morphological characteristics. Further study of *Ceratopteris* in South America is needed. Specimens from Florida, USA (*Lakela & DeBoer 2922* [NY, US], *Sutherland 3159* [US]) show mixed features of *C. thalictroides*, *C. gaudichaudii* and *C. oblongiloba* (see below) in leaf morphology, possibly due to submergence or flotation. Further investigation of *Ceratopteris* in that region is also needed.

2. **Ceratopteris gaudichaudii** Brongn. var. **gaudichaudii**

C. gaudichaudii Brongn., Bull. Sci. Soc. Philom. Paris, sér. 3, 8: 187 (1821); Wagner & Grether, Occas. Pap. B. P. Bishop Mus. 19: 77 (1948); Fosberg, Amer. Fern J. 48: 35 (1958). —*Type.* Guam, Agaña River, *Gaudichaud 83* (syn- FI, G, P [photo!]).

Plants annual, semi-aquatic or aquatic, rooting, sometimes floating. *Rhizomes* reduced. *Roots* at stipe base. *Scales* sparse on stipe, brownish-hyaline, sessile, broadly ovate to peltate with gently curved margins, lamina thin, composed of sinuous cells. *Leaves* dimorphic. *Sterile leaves* 5–18 cm long, held obliquely to patently, green, softly herbaceous, highly gemmiferous at sinuses of segments; stipes 1/3–3/4 length of blade, semicircular to trapezoid; blades 4–12 cm long, 3–8 cm wide at base, narrowly triangular, 2–4-dissected, mostly pinnatifid; pinnae 5–8 pairs, alternate, basal pinnae 2–5 cm long, 1.5–4 cm wide, triangular to narrowly triangular, with short stalk; pinnules 2–4 pairs, alternate, base broadly decurrent; terminal lobes often dentate, narrowly deltoid to narrowly oblong, apex acute; oblong terminal lobes to 2 cm long, 0.3 cm wide; veins anastomosing, without veinlet in areole. *Fertile leaves* 10–25 cm long, oblique to patent, brownish at maturity; stipes 1/3–2/3 length of blade; blades 6–20 cm long, 5–13 cm wide at base, narrowly triangular, 3–4-dissected, 0–2-pinnate; pinna 4–9 pairs, with short stalk, alternate, basal pinnae 3–7 cm long, 3–5 cm wide, triangular; terminal lobes to 5 cm long, 0.2 cm wide, linear, margin thin, reflexed toward costa enclosing sori. *Sporangia* subsessile; annulus vertical, with 35–50 broad incrassate cells and 7–9 broad lip cells. *Spores* 32 per sporangium, tetrahedral, 95–140 μm in distal diam., with thick parallel-muri on surface. *Chromosomes* $n = 78$, tetraploid. *Nucleotide sequence of rbcL gene* AB059575 registered in INSD.

Distribution. **Oceania**: Guam.

Habitat. Swamps, small streams, irrigation ditches, taro patches.

Representative specimens examined. GUAM: Agaña Spring, *Evans 628* (US); Agaña Swamp, *Manner LR28897* (GUAM); Agaña Swamp, *Masuyama 3250* (GUAM); Almagosa, Naval Magazine, *Stone 4900* (GUAM); Bonya Spring, *Raulerson 15654* (US); Mt. Almagosa, Chepak Springs, *Stone 4321* (GUAM); Talofofo River, *Grether 4326* (UC, US); Ugum River above Talofofo Falls, *Rinehart LR25144* (GUAM).

Notes. Brongniart (1821) recognized two species, *Ceratopteris thalictroides* and *C. gaudichaudii*, when he proposed the genus *Ceratopteris*. Wagner & Grether (1948) and Fosberg (1958) also regarded *C. gaudichaudii* as a distinct species, whereas DeVol (1967) and Lloyd (1974) included *C. gaudichaudii* within *C. thalictroides*. Recently, based on chloroplast DNA data and chromosome number, Masuyama & Adjie (2008) regarded *C. gaudichaudii* as belonging to the north type, the type different from *C. thalictroides* (Masuyama *et al.* 2002).

As in Brongniart's species description, the sterile lobes of *C. gaudichaudii* are narrowly oblong and acute. Wagner & Grether (1948) regarded this as an important diagnostic character to separate *C. gaudichaudii* from *C. thalictroides*. *C. gaudichaudii* is also characterized by the somewhat dentate margins of lobes, as Fosberg (1958) noted. This feature results from frequent gemma formation at lobe sinuses. These two characters do not seem inducible in floating or underwater conditions, because such characters did not occur in cultivated floating sporophytes of var. *vulgaris* (see below) from Guam.

The distribution of var. *gaudichaudii* is very limited and the morphology is much specialized, compared with var. *vulgaris*.

3. **Ceratopteris gaudichaudii** Brongn. var. **vulgaris** Masuyama & Watano, **var. nov.** —Fig. 1

Haec varietas a *C. gaudichaudii* var. *gaudichaudii* foliis sterilibus minus gemmiferis, lobis integris apice acutis vel obtusis differt; a *C. thalictroide* foliis sterilibus aliquantum tenuioribus, stipite quam lamina semper breviore et pinnis densis differt.

Typus. Japan, Chiba Pref., Nagareyama, Nishifukai, at a deserted rice paddy, alt. ca. 20 m, *S. Masuyama 3260* (holo- TNS; iso- KYO, TI).

Plants annual, semi-aquatic, rooting. *Rhizomes* reduced. *Leaves* dimorphic, sparsely scaly. *Sterile leaves* 5–40 cm long, held obliquely, gemmiferous at sinuses of segments; stipes 1/3–3/4 length of blade; blades 4–30 cm long, 3–12 cm wide at base, narrowly ovate to narrowly triangular, 2–4-dissected, mostly pinnatifid; pinnae 3–9 pairs, alternate, basal pinnae 1–12 cm long, 1–8 cm wide, ovate to triangular to narrowly triangular, with short stalk; pinnules 1–4 pairs; terminal lobes entire, ovate to deltoid to oblong, apex acute or obtuse; oblong terminal lobes to 1.5 cm long, 0.7 cm wide. *Fertile leaves* 10–50 cm long, oblique to patent; stipes 1/3 to equal length of blade; blades 5–35 cm long, 5–20 cm wide at base, narrowly triangular to triangular, 1–4-dissected, 0–3-pinnate; pinna 3–10 pairs, with short stalk, alternate, basal pinnae 3–16 cm long, 3–14 cm wide, triangular to widely triangular; terminal lobes to 10 cm long, 0.2 cm wide, linear. *Sporangia* subsessile, annulus vertical, with 35–60 broad incrassate cells and 6–10 broad lip cells. *Spores* 32 per sporangium, 90–135 μm in distal diam. *Chromosomes* $n = 78$, $2n = 156$; tetraploid. *Nucleotide sequence of rbcL gene* AB059573 and AB059575 registered in INSD.

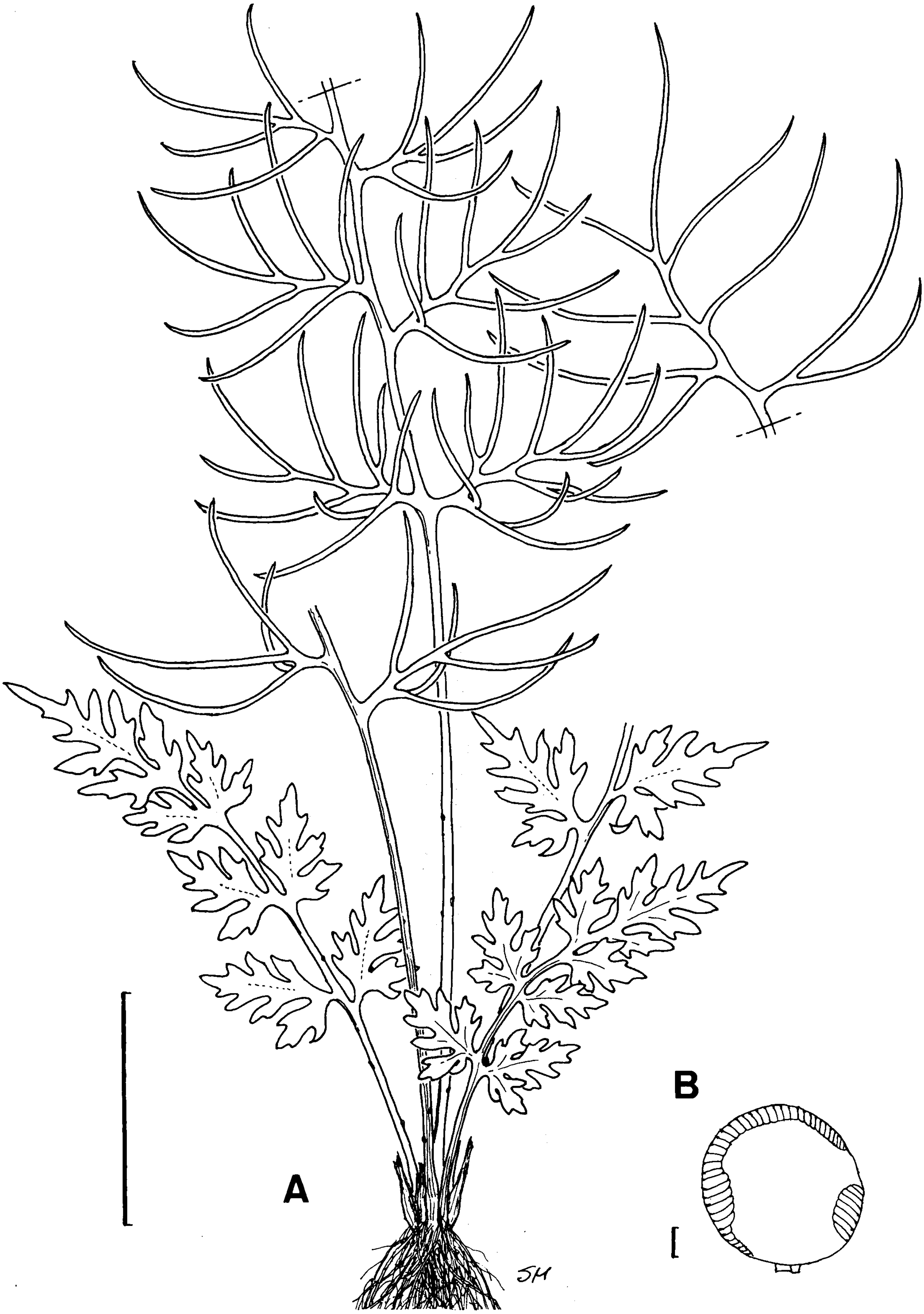

FIG. 1. *Ceratopteris gaudichaudii* var. *vulgaris* (*Masuyama 3260*, type). A: Sporophyte. B: Sporangium. Scale bar = 5 cm (A); 0.1 mm (B).

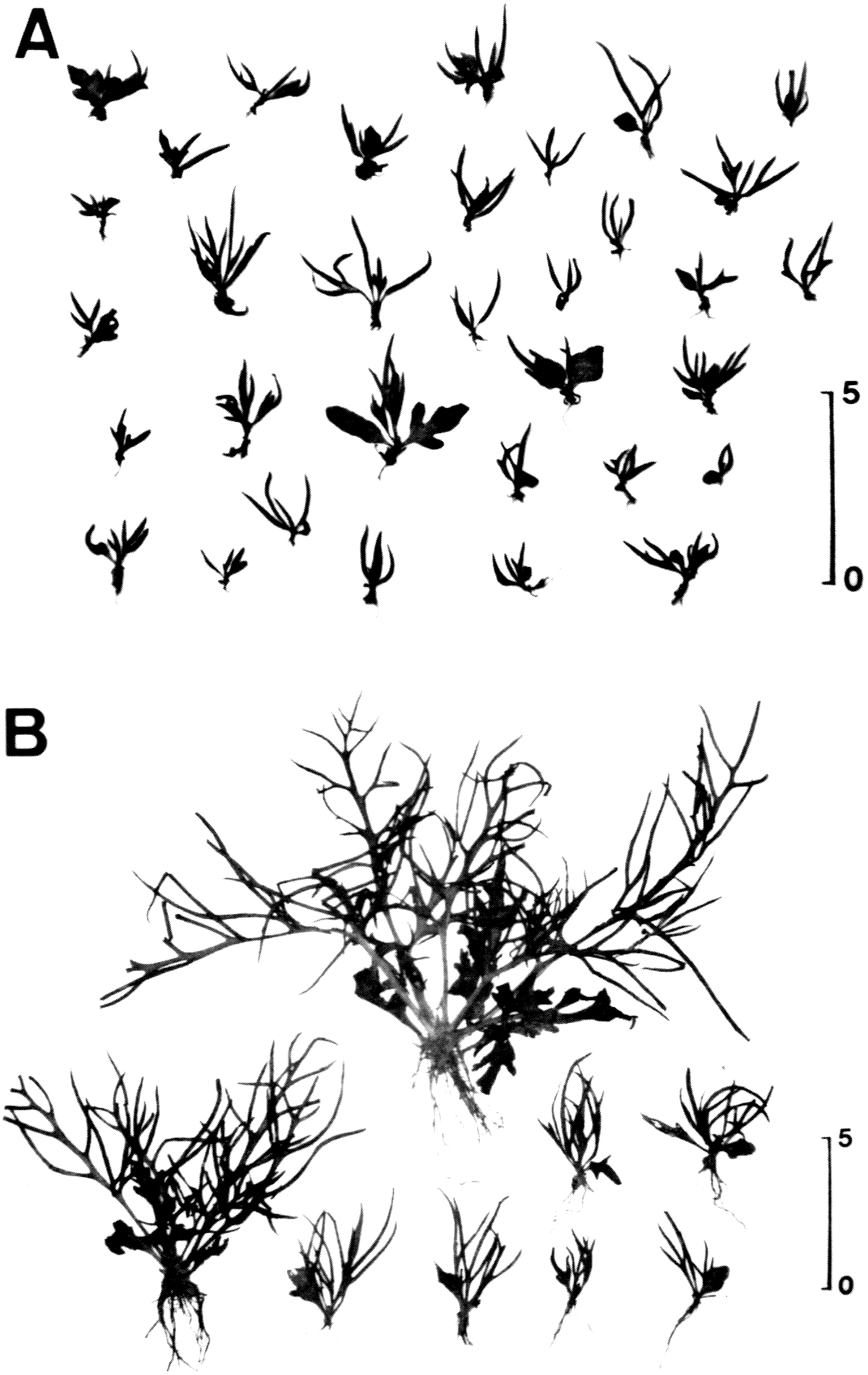

FIG. 2. Specimens from a population of small sporophytes (A) and both small and large sporophytes (B) of *Ceratopteris gaudichaudii* var. *vulgaris*. A, *Masuyama 2090*; B, *Masuyama 695*. Scales in cm.

Japanese name. Hime-mizuwarabi (nov.).

Distribution. **Asia**: China (C., S.), Japan (C.), Korea (S.), Nepal, Taiwan. **Oceania**: Guam, Hawaii.

Habitat. Rice paddies, taro patches, irrigation ditches.

Representative specimens examined. CHINA: Anhui, *Maekawa s.n.* (TI); Hainan, Hung Mo Shan, *Tsang & Fung 490* (UC); Hong Kong, Lantao Isl., *Taam 2187* (KYO); Nankin, Suan-tze, *Ching 7787* (NY, UC, US).

GUAM: Yigo, Mt. Santa Rosa, *Masuyama 2964* (GUAM).

HAWAII: Oahu, Punaluu, *Ozaki 1572* (US); Oahu, *Degner 3709* (NY).

JAPAN: Chiba, Abiko, *Murata & Togashi s.n.* (KYO, UC); Chiba, Kamagaya, *Ohba 67126* (TI); Chiba, Kashiwa, *Masuyama 689* (TNS); Chiba, Kashiwa, *Masuyama 877* (TNS); Chiba, Nagareyama, *Masuyama 730* (TNS); Chiba, Nagareyama, *Masuyama 881* (TNS); Chiba, Nagareyama, *Masuyama 1290* (TNS); Chiba, Nagareyama, *Masuyama 3260* (KYO, TI, TNS); Kanazawa, Izumi-asahi, *Fukuoka s.n.* (KYO); Fukui, Mikata, *Kadono 589* (KYO); Shizuoka, Fuji, *Masuyama 710* (TNS); Shizuoka, Fuji, *Masuyama 2542* (TNS); Shizuoka, Yawata, *Sugimoto s.n.* (KYO); Tanba, Minamikuwata, *Araki 1481* (KYO); Gifu, Hozumi, *Masuyama 695* (TNS); Gifu, Hozumi, *Masuyama 2090* (TNS); Kyoto, Chushojima, *Tagawa 7173* (KYO, UC); Kyoto, Yawata, *Murata 67339* (KYO); Hyogo, Kinosaki, *Kurosaki & Miyake 1971* (TI); Osaka, Hirano, *Kodama 3532* (KYO); Osaka, Neyagawa, *Seto 7330* (KYO, TI, UC, US); Hiroshima, Fukuyama, *Matsumoto 1141* (KYO); Tokushima, Anan, *Masuyama 1439* (TNS); Tokushima, Anan, *Masuyama 1441* (TNS); Kochi, Kochi, *Masuyama 1421* (TNS); Kumamoto, Gazu, *Shimada 11603* (KYO); Kumamoto, Kikuchi, *Makino MH32998* (KYO); Satsuma, Ibusuki, *Yajima s.n.* (TI); Kagoshima, Amami Isl., Akimyou, *Masuyama 2135* (TNS); Kagoshima, Amami Isl., Yanyu, *Masuyama 2130* (TNS); Kagoshima, Amami Isl., Yanyu, *Masuyama 2131* (TNS); Kagoshima, Fukiage, *Masuyama 1291* (TNS); Kagoshima, Tanegashima Isl., Shimonaka, *Masuyama 2218* (TNS); Kagoshima, Tokunoshima Isl., Inokawa, *Masuyama 2187* (TNS); Kagoshima, Tokunoshima Isl., *Tagawa & Iwatsuki 2551* (US); Okinawa, Okinawa Isl., Oyama, *Masuyama 2099* (TNS).

KOREA: Cholla Namdo, Sunchon, *Chang 3142* (KYO).

NEPAL: Dumhan, *Hara & al. 6305181* (KYO, TI); Khebang through Bharomdin, *Hara & al. 6305182* (KYO, TI); Simul Bari, *Biswas 8700* (KYO).

TAIWAN: Taihoku, Shizangan, *Shimozawa 734* (KYO).

Notes. This group corresponds to the north type reported by Masuyama *et al.* (2002), to which *Ceratopteris gaudichaudii* Brongn. belongs, but its morphology is not so specialized as *C. gaudichaudii*. They are therefore separated at the variety rank.

Lloyd (1974) noted that extremely small plants in Japan, as exemplified by *Murata & Togashi s.n.* (UC 302600), might be taxonomically problematical. In Japan, except for Okinawa, we often found populations composed of plants far smaller than that specimen (*Masuyama 689* [TNS], *Masuyama 730* [TNS], *Masuyama 1439* [TNS], *Masuyama 2090* [TNS], *Masuyama 2135* [TNS], *Masuyama 2542* [TNS]) (Fig. 2A). Near those, other populations with both extremely small and much larger plants were also found (*Masuyama 695* [TNS], *Masuyama 710* [TNS], *Masuyama 1290* [TNS], *Masuyama 1441* [TNS], *Masuyama 2131* [TNS]) (Fig. 2B). Because plants in Japan except Okinawa have allozyme compositions of the north type (Watano and Masuyama 1994), the extremely small plants are considered to be dwarf forms of var. *vulgaris*. Since plants of the north type tend to reduce the vegetative phase by low temperature and short day (Masuyama 1996), such dwarfism may easily occur. Small plants have been collected also in the Himalayan region (*Biswas 8700* [KYO]; *Hara & al. 6305181*, [KYO, TI]), Central China (*Maekawa s.n.* [TI]) and Korea (*Chang 3142* [KYO]).

Large plants in Japan that Lloyd (1974) noted to be taxonomically problematical are probably represented by *Seto 7330* (KYO, TI, UC, US). *Araki 1481* (KYO), *Kurosaki & Miyake 1971* (TI) and *Makino MH32998* (KYO) are similar in size and morphology to that specimen. Considering that they were collected in the regions occupied by the north type (see Watano & Masuyama 1994), they can be regarded as large forms of var. *vulgaris* that were growing under special environmental conditions. We occasionally found extraordinarily large plants (*Masuyama 877* [TNS], *Masuyama 1290* [TNS], *Masuyama 2130* [TNS]) in deserted paddy fields and irrigation ditches, the sites under little artificial disturbance.

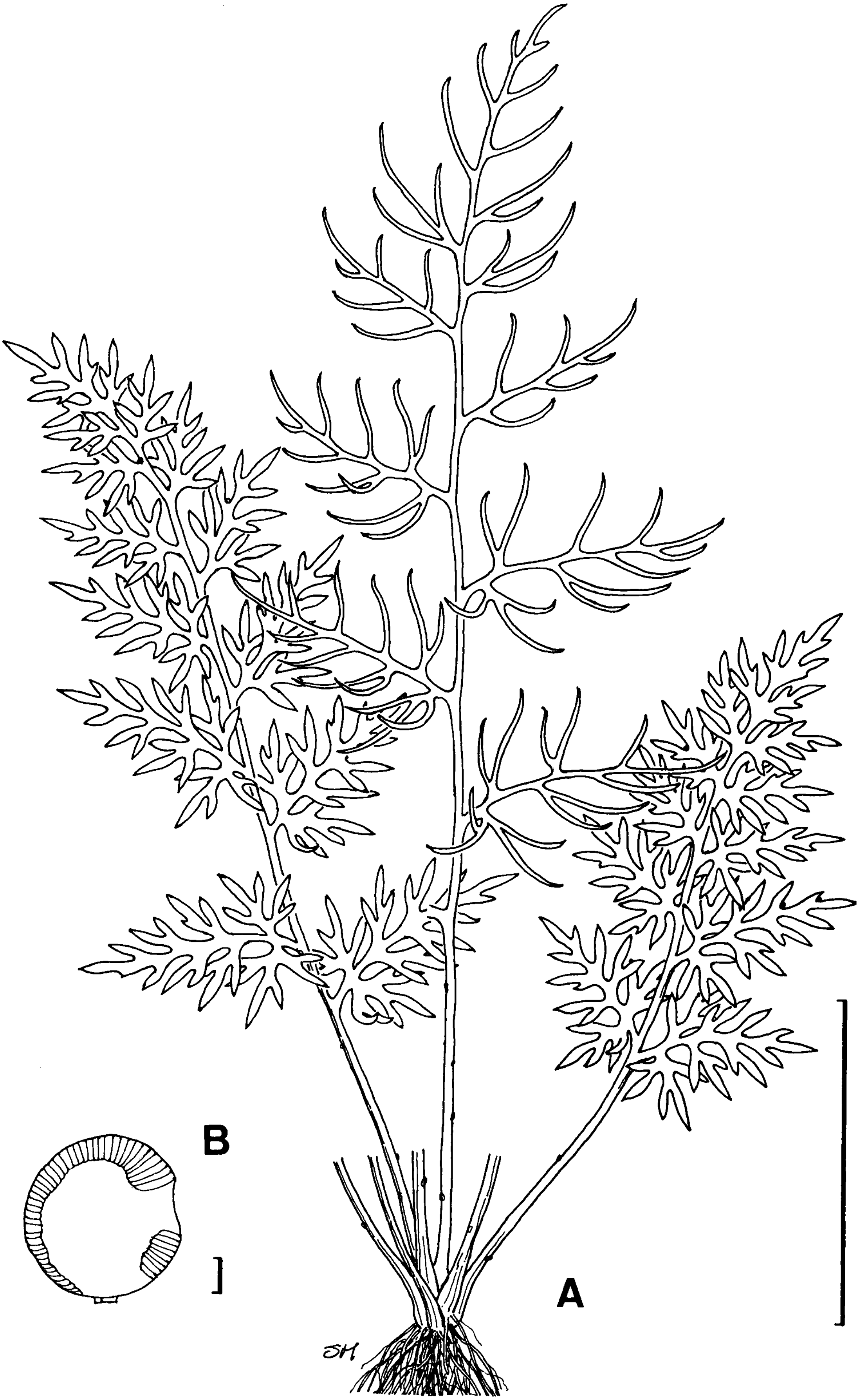

FIG. 3. *Ceratopteris oblongiloba* (*Masuyama 3197*, type). A: Sporophyte. B: Sporangium. Scale bar = 5 cm (A); 0.1 mm (B).

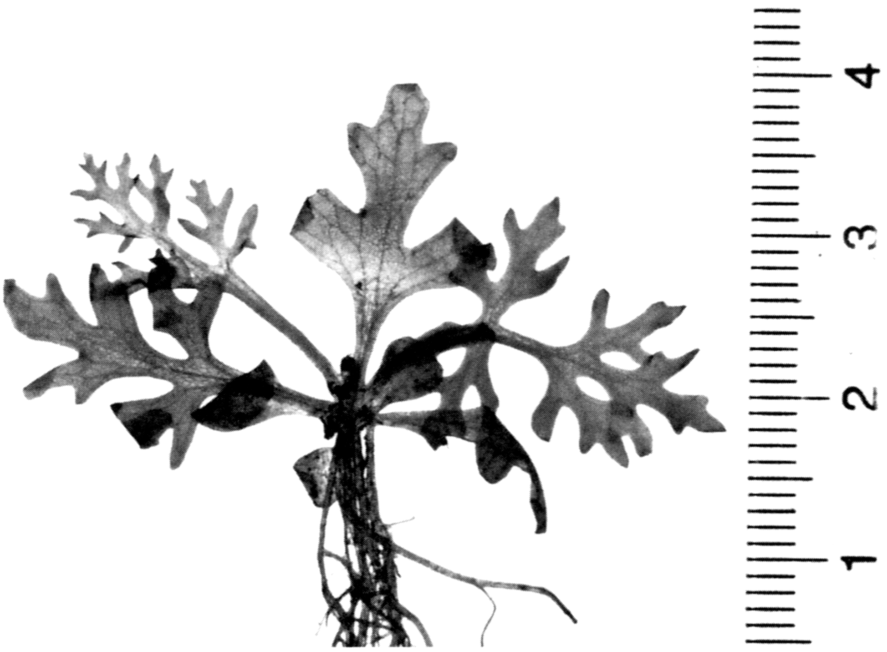

FIG. 4. Juvenile sporophyte of *Ceratopteris oblongiloba* (*Masuyama 3196*). Scale in cm.

4. **Ceratopteris oblongiloba** Masuyama & Watano, **sp. nov.**—Fig. 3

Haec species a *C. gaudichaudii* var. *gaudichaudii* foliis sterilibus minus gemmiferis, lobis integris apice acutis vel obtusis, pinnulis densis et lobis terminalibus parvis anguste deltoideis vel anguste oblongis differt; a *C. thalictroide* foliis sterilibus aliquantum tenuioribus, stipite quam lamina semper breviore et pinnis densis differt.

Typus. Indonesia, Java, Bogor, Bubulok, Babakan, on wet ground of taro patches, alt. ca. 100 m, *S. Masuyama 3197* (holo- BO; iso- KYO, TNS).

Plants annual, semi-aquatic, rooting. *Rhizomes* reduced. *Roots* at stipe base. *Scales* sparse on stipe, brownish-hyaline, sessile, broadly ovate to peltate with gently curved margins, lamina thin, composed of sinuous cells. *Leaves* dimorphic. *Sterile leaves* 5–25 cm long, held obliquely, green, softly herbaceous, gemmiferous at sinuses of segments; stipes 1/3–3/4 length of blade, semicircular to trapezoid; blades 4–15 cm long, 3–8 cm wide at base, narrowly ovate to narrowly triangular, 2–5-dissected, 1-pinnate; pinnae 3–9 pairs, alternate, basal pinnae 1–4 cm long, 1–3 cm wide, ovate to triangular to narrowly triangular, with short stalk; pinnules 2–5 pairs, alternate, base broadly decurrent; terminal lobes entire, small, narrowly deltoid to narrowly oblong, apex acute or obtuse; oblong terminal lobes to 2 cm long, 0.3 cm wide; veins anastomosing, without veinlet in areole. *Fertile leaves* 10–40 cm long, oblique, brownish at maturity; stipes 1/3 to equal length of blade; blades 5–25 cm long, 3–10 cm wide at base, narrowly triangular, 1–4-dissected, 1–2-pinnate; pinna 4–8 pairs, with short stalk, alternate, basal pinnae 2–10 cm long, 2–6 cm wide, triangular; terminal lobes to 5 cm long, 0.2 cm wide, linear, margin thin, reflexed toward costa enclosing sori. *Sporangia* subsessile; annulus vertical, with 35–50 broad incrassate cells and 6–9 broad lip cells. *Spores* 32 per sporangium, tetrahedral, 95–145 μm in distal diam., with thick parallel-muri on surface. *Chromosomes* $n = 78$, $2n = 156$; tetraploid. *Nucleotide sequence of rbcL gene* AB059576 registered in INSD.

Distribution. **Asia**: Cambodia, Indonesia (Sumatra, Java), Philippines (Luzon), Thailand (Malay P.).

Habitat. Rice paddies, taro patches, irrigation ditches, small streams.

Representative specimens examined. CAMBODIA: Cambodge, *Couderg s.n.* (UC).

INDONESIA: Java, Bogor, *Masuyama 2600* (BO, KYO, TNS); Java, Bogor, *Masuyama 2603* (BO, TNS); Java, Bogor, *Masuyama 3196* (TNS); Java, Bogor, *Masuyama 3197* (BO, KYO, TNS); Java, Bogor, *Masuyama 3198* (BO); Sumatra, Djambi, *Posthumus 934* (BO); Sumatra, Ranan, *Van Steenis 3332* (BO); Sumatra, Telug Kabung, *Borssum 1526* (BO).

PHILIPPINES: Luzon, Rizal, *Ramos 2062* (US).

THAILAND: Ranong, Kaper, *Shimizu & al. T-26420 & T-26482* (KYO).

Note. Ceratopteris oblongiloba corresponds to the third type reported by Masuyama *et al.* (2002). Lloyd (1974) did not refer to this species. In general, plants are highly dissected: in juveniles, dissection starts even at the fourth or fifth leaf and goes on two times at the sixth leaf or so (Fig. 4), and leaves of adults are mostly characterized by dense pinnules on pinna-rachis. *C. oblongiloba* is common in Java Island, Indonesia.

5. **Ceratopteris froesii** Brade

C. froesii Brade, Arch. Jard. Bot. Rio de Janeiro 18: 31 (1964). —*Type*: Brazil, Região do Araguaia, Campos Gerais de Andorinha, Estado do Pará, *R. L. Froes 29906* (holo- IAN [photo!]).

Distribution. **South America**: Brazil (N.).

Note. According to the species description and drawing by Brade (1964), the sterile leaves are less than 3 cm long and at most trilobed with obtuse to rounded apex, while the fertile leaves are less than 4 cm long and have at most two pairs of pinnae. Although *Ceratopteris froesii* was considered to be a dwarf form of *C. deltoidea* (*C. richardii* in the sense of Lloyd), Brade noted that it was unlikely because the obtuse to rounded shape of the lobes and weak dissection of the leaves did not change under cultivation. Lloyd (1974) regarded *C. froesii* as a synonym of *C. thalictroides*. However, because of its distinct morphology, it is hard to link this species with either of *C. thalictroides* s.str., *C. gaudichaudii* or *C. oblongiloba*. *C. froesii* is therefore provisionally treated as a distinct species pending molecular and cytological analyses.

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